STUDIES IN SUBLITTORAL ECOLOGY

III. Laminaria Forest on the West Coast of Scotland; A Study of Zonation in Relation to Wave Action and Illumination

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Introduction

Rocky areas of the sea bottom in the shallow sublittoral region of the coast of Britain are in general densely covered with a forest of brown laminarian seaweeds. In this paper an account is given of the influence of depth on the distribution of organisms within the *Laminaria* forest, and of the factors which mainly control this distribution. Observations were made by means of a diving helmet (see Kitching, Macan, and Gilson, 1934), from low water of spring tides to a depth of about 12 meters below this level.

Carsaig Island, the place chosen for this work, is about 1 km. long and 1/5 km. wide, and lies in the Sound of Jura, on the west coast of Scotland (see inset to Fig. 1). The waters of the Sound of Jura in general reach a depth of 100–200 meters, and the tidal currents attain a velocity of 7–8 km. per hour; in windy weather there is a short choppy sea. According to measurements made in open water during hot still weather, the gradient of temperature within the shallow sublittoral region is insignificant; and it is probable that gradients of salinity, oxygen content, carbon dioxide content, and hydrogen ion concentration must also be slight. However, in places sheltered from wave action such gradients may well be set up. The western shore of Carsaig Island is fully exposed to wave action, but the eastern side is well protected. As will be shown below, the main features of the distribution of organisms within the shallow sublittoral region may reasonably be attributed to gradients of wave action, with all its consequences, and to illumination.

Distribution in the Laminaria Forest

Introduction and Methods

The *Laminaria* forest was investigated by observation from a boat with the help of a water telescope all around the coast of Carsaig Island, and by diving at several selected stations. Finally a detailed study was made, by diving, at one station (*A* on map, Fig. 1), down to a depth of about twelve meters below low water of spring tides. At this last station data were collected for the drawing of a diagrammatic section (Fig. 1) to show the vertical distribution of algae. Investigations were carried on in September of 1932, and in August of 1933–1936 inclusive. The general description which follows is based on all these observations.

Dominant Large Brown Algae

The upper margin of the sublittoral region,—that part which lies just above low water of spring tides,—is very different in character from

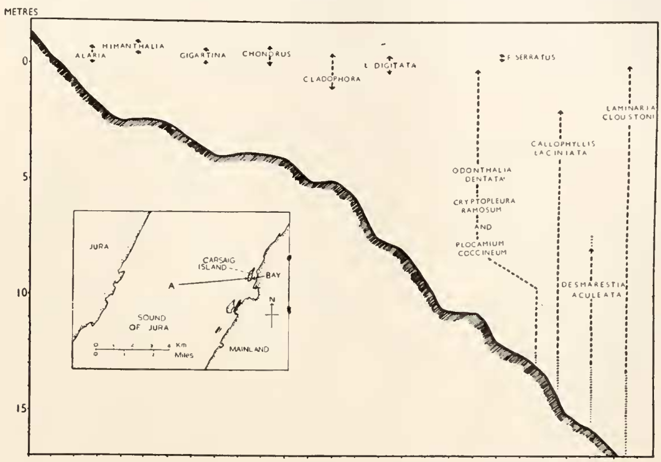

FIG. 1. Section at position *A* (see inset) on coast of Carsaig Island. Inset: map showing position of Carsaig Island in Sound of Jura, Argyll, Scotland.

the deeper layers. It is dominated by three large brown algae, *Himanthalia lorea, Alaria esculenta,* and *Laminaria digitata* (see Fig. 1). *Alaria* is confined to the west side of the island, and favors vertical rock surfaces as well as wave action. *L. digitata* and *Himanthalia* range all around the island. All three grow sufficiently densely to protect the organisms amongst them to a large extent from desiccation, so that the associated fauna is typically sublittoral.

Just below low water of spring tides lies the lower limit of *Laminaria digitata,* and, except in extreme shelter, the upper limit of *Laminaria Cloustoni.* There is very little mixing of the two species. *Laminaria Cloustoni* in its zone forms a dense forest, but does not reach its greatest size at depths less than 4 meters. Here the innumerable vertical stipes support an immense canopy of fronds, below which the light is dim even when the sun is shining brightly above. In order to penetrate this forest without risk of the air line becoming entangled, we had to cut a glade with shears. The forest reaches a height of about 3 meters above the bottom. Individual plants of *L. Cloustoni* reach a length of 2 meters or more, the longest measured being 2.40 meters; and scattered plants of *Saccorhiza bulbosa* reach about the same length. The full height of the forest is made up by epiphytic *Laminaria* plants growing on the stipes of *L. Cloustoni*. These epiphytic plants are chiefly *L. digitata*, which, however, is rarely if ever found growing directly on the sea bottom below its normal zone. In general *Laminaria* spp. from deeper down or from the sheltered side of the island were found to have un-

TABLE I

Population of Laminaria digitata from the sublittoral fringe

	Individuals per 5 square meters of frond	Individuals per 10 stipes	Individuals per 10 holdfasts
On east (sheltered) side of Carsaig Island:			
Patina pellucida	31	0	1
Spirorbis spp.	6800	6	599
Scrupocellaria reptans	45	0	0
On west (wave-exposed) side of Carsaig Island:			
Patina pellucida	131	8	10
Spirorbis spp.	0	0	652
Scrupocellaria reptans	0	0	2

divided or incompletely divided fronds, in contrast to the plants growing nearer the surface and on the wave-exposed side. Presumably wave action is most vigorous near the surface of the water.

Between 6 and 12 meters below low water of spring tides the forest opens out, so that it was possible to walk between the *Laminaria* plants easily in spite of the rugged nature of the sea bottom; we therefore called this area the "park." In the park nearly every *L. Cloustoni* was entwined with a large unattached plant of the brown alga *Desmarestia aculeata*. Although 12 meters was the greatest depth to which we penetrated, it was possible through the misty water to see the park extending downwards much further on the steeply sloping bottom.

In extreme shelter from wave action *L. Cloustoni* is replaced by *L. saccharina*, or by a form, allied to this species, which is characteristic of the sea lochs of the west coast of Scotland (Kitching, 1935). The latter extends up to the lower margin of the zone of *L. digitata* in the extreme shelter of the small bay on the eastern side of the island, but southwards with increasing wave action it is progressively replaced from above by *L. Cloustoni.*

Associated Flora and Fauna

The canopy of *Laminaria* fronds is relatively clean of epiphytic algae in shallow water on the western side of Carsaig Island; instead it carries many colonies of the hydroid *Obelia geniculata* and the polyzoan *Membranipora membranacea,* and numerous gastropods, including *Patina pellucida.* On the more sheltered eastern side of the island *Obelia* and *M. membranacea* are much less abundant; they are practically confined to a narrow zone at the level of low water of spring tides, and they are absent from the very sheltered Bay (see map in Fig. 1); whereas in shelter filamentous epiphytes with their associated fauna, and the tube-worm, *Spirorbis* (spp.), and the polyzoan, *Scrupocellaria reptans,* may cover nearly all the space available on the *Laminaria* fronds. These same differences, though in lesser degree, may be observed at greater depths on the wave-exposed western side of the island. Here again it may reasonably be claimed that depth affords shelter from wave action.

The undergrowth of the sublittoral fringe consists mainly of the green alga *Cladophora rupestris* and the red algae *Chondrus crispus, Gigartina stellata,* and *Rhodymenia palmata.* Of these *Cladophora* and *Rhodymenia* also grow as epiphytes on the uppermost parts of the stipes of *Laminaria Cloustoni* in shallow water only, and small plants of *Rhodymenia* are sometimes found attached to the tips of *Laminaria* fronds in shallow water. The distribution of these algae is such as to suggest that they require a relatively high incidence of light.

The holdfasts and stipes of the *Laminaria Cloustoni* plants, except the upper parts of those nearest to the surface of the water, and the rock bottom between the holdfasts, are densely covered with an undergrowth of red algae, which includes *Membranoptera alata, Phycodrys rubens, Odonthalia dentata, Delesseria sanguinea, Ptilota plumosa,* and *Cryptopleura ramosum. Callophyllis laciniata* flourishes especially in the park, where its bright red fronds may be seen from afar. Apart from this, the composition of the undergrowth appears uniform from 2 to 12 meters. All these algae appear to favor a relatively weak illumination, a conclusion which is supported by photoelectric measurements reported later in this paper (Table II).

The tube-worms *Spirorbis* spp. and *Salmacina incrustans,* as well as various polyzoans and colonial tunicates, are abundant on the inner parts of the *Laminaria* holdfasts, even in places well exposed to wave action;

but the outer surfaces of these holdfasts are usually clean. The holdfasts shelter an extensive motile fauna, which will not be described in this paper. The composition of this fauna did not appear to be significantly influenced by depth within the limits of our exploration.

Recolonization of Denuded Areas of Laminaria *Forest*

In August, 1936 we were able to examine areas where the *Laminaria* forest had been cut down with shears 12 months previously. The old holdfasts had disappeared, and new *Laminaria Cloustoni* plants covered the area very densely, and had grown to a height of about 1 meter. The holdfasts were affixed very tightly to the rock. They were almost clean of epibiotic organisms, but a few specimens of *Spirorbis* were found on

TABLE II

Position of sea photometer	Depth below water surface (meters)	Illumination cut off by seaweeds (per cent)
Under *Saccorhiza*, near *Callophyllis*	4.0	99.5
Among *Chondrus* and *Cladophora*, in zone of *Laminaria digitata*	1.5	48
At bottom, in old forest	3.9	98.7–99.4
Under dense new growth of *L. Cloustoni*, one year old	4.0	99.1–99.5
Under *Laminaria Cloustoni* in "park"	11	82–85
Under old *L. Cloustoni* forest	4.0	98.8–99.1

The first four observations listed above were made on August 13, 1936, between 12.25 and 1.00 P.M. G.M.T., under an overcast sky. The last two observations were made on August 22, 1936, between 2:08 and 3:15 P.M., under a sunny sky with light cirrhus cloud. On both days the wind was light, the water temperature about 12.5–12.6° C., and the air temperature 15–16° C. All these observations were made at station *A* (Fig. 1).

them. Some *Patina* were found on the stipes and fronds, but little else. The motile fauna associated with these young *Laminaria* plants was much poorer in numbers than that of the older forest, but was in general similar in constitution.

ILLUMINATION IN THE LAMINARIA FOREST

Apparatus and Methods

Measurements of the light intensity at a number of positions in the *Laminaria* forest were made photoelectrically, according to the general methods described by Atkins and Poole (1933). The light intensities in air and at a chosen under-water position were measured simultaneously and compared. Two "photronic" rectifier cells, made by the

Weston Electric Company, were employed. Separate galvanometers were used for the two cells, as this was found to be an advantage in changeable light, and also reduced the time during which the diver had to wait in the cold while readings were being taken. The cells were mounted in water-tight containers, and could be screened either with a flashed opal glass alone or with a selected color filter [1] underneath an opal glass.

The two cells were kindly calibrated for me by Dr. W. R. G. Atkins of the Marine Biological Laboratory, Plymouth. The calibrations were carried out by daylight under a variety of light intensities, with the cells mounted ready for use but dry, and under opal glass without color filters. Submersion under a thin film of water made scarcely any difference. For low light intensities, and with the low external resistance used, the relation between current and light intensity was approximately linear. For most purposes 10 ohm pattern L galvanometers made by the Cambridge Instrument Company were used, but for very low light intensities, as recorded in the depths of the *Laminaria* forest, it was necessary to use a 1000 ohm pattern LY galvanometer; however, at these low intensities of light the linear relation noted above was found still to hold in spite of the increased resistance of the external circuit.

It is recognized that the lux is not an ideal unit for present purposes; and that the measurement of illumination over a wide spectral range, with a photocell differentially sensitive with respect to wave-length, is not an entirely satisfactory procedure. However, it is believed that these objections do not invalidate the treatment of results which will be followed below.

Results

As a result of observations made with the opal screen alone, the light intensity in various situations in the *Laminaria* forest was found to be only a very small fraction of that in air. A comparison was then made of the light intensities within the forest and in open water at the same depth by using curves obtained in open water (Fig. 2). In this way the light intensity within the forest was expressed as a percentage of what it would have been had there been no forest, and from this was computed the percentage illumination cut off by the forest. A few typical results are given in Table II. In general the forest cut off about 99 per cent of the available light, and new growth one year old was about as effective. However, in the park, only 82–85 per cent was cut off by the seaweeds, and the illumination at the bottom was better than in the

[1] Listed by the makers (Schott and Gen, of Jena) as BG 12 (blue, 2 mm. thick), VG 2 (green, 4 mm.), RG 1 (light red, 2 mm.), and RG 8 (dark red, 2 mm.).

forest, even though the depth was greater. It is not possible to say to what extent this condition is general on the British coast.

The illumination at any one position in the forest fluctuates continually owing to the movement of the fronds overhead. Therefore it was

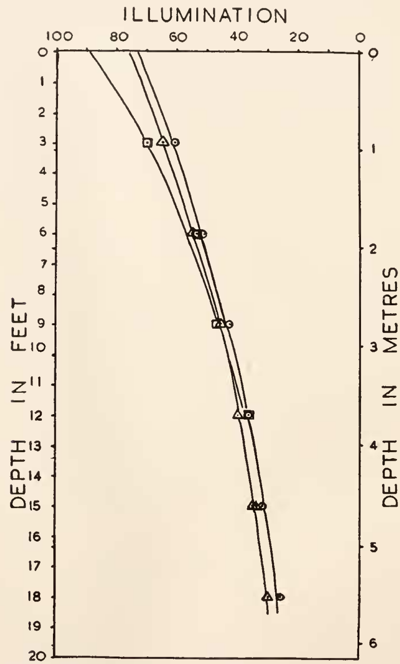

FIG. 2. Graph showing illumination at various depths in open water at position *A*, on the west side of Carsaig Island (see inset to Fig. 1). A plain opal glass, without color filters, was used. The illumination in air is rated as 100.

⊡ August 12, 1936 (transmission 79–81 per cent per meter).
△ August 13, 1936 (transmission 80–87 per cent per meter).
⊙ August 19, 1936 (transmission 81–85 per cent per meter).

found impossible with our equipment to investigate in detail the quality of the light in the forest, as compared with that in open water. However, since the *Laminaria* fronds are opaque and of a darkish brown color, it seems probable that not much light of any wave-length is either transmitted or reflected into the depths of the forest by the fronds; presumably most of that which reaches the depths of the forest passes between the fronds. Therefore, results obtained with the opal alone probably represent approximately the fraction of light of any wave-length which penetrates the forest, as compared with the illumination at that wave-length in the same depth of open water. It is therefore possible to estimate approximately the depths in open water at which the monochromatic illumination at various frequencies is equivalent to that in the *Laminaria* forest just below low water mark. For this somewhat rough

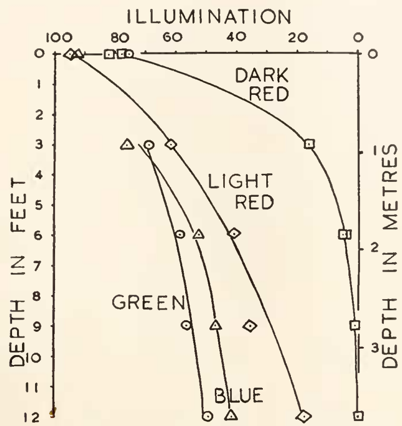

FIG. 3. Graph showing illumination at various depths in open water at position *A*, on the west side of Carsaig Island (see inset to Fig. 1). Color filters were used in addition to opal glass. The illumination in air is rated as 100. The observations were made on August 19, 1936.

Blue, 350–470 mμ, transmission 75–91 per cent per meter.
Green, 500–570 mμ, transmission 87–93 per cent per meter.
Light red, 620–700 mμ, transmission 53–65 per cent per meter.
Dark red, 700–750 mμ, transmission 27–28 per cent per meter.

and arbitrary procedure the illumination in the *Laminaria* forest has been taken as 1 per cent of that in open water at the same depth, and the transmission for light of various wave-lengths has been given the values obtained from Fig. 3, although indeed transmission may actually vary with depth. The results of this calculation are given in Table III, and are discussed further on (p. 334). The preferential transmission of green light is in accord with the results of many other workers in coastal waters (Knudsen, 1922; Atkins, 1926; Klugh, 1927; Clarke, 1936, 1939).

Discussion of Zonation

The zonation of plants and animals is very strongly marked in the littoral region of the British coast. The dominant algae are restricted very obviously to narrow belts along the shore; while the zonation of animals, although usually less precise, is fully shown by studies of population density and growth rate (Fischer-Piette, 1936; Moore, 1934). Littoral zonation may reasonably be attributed in the main to desiccation (Baker, 1910; Muenscher, 1915; Kanda, 1916; Johnson and Skutch, 1928; and Hatton, 1930, 1932), although in general decisive proof has not yet been given, and to a smaller degree to the effects of heat and light (Gail, 1919, 1922; Klugh and Martin, 1927). In response to the severe gradation of the controlling environmental factors, the zonation of organisms in the littoral region is sharply defined.

At the upper margin of the sublittoral region, along a strip of shore only uncovered at low water of spring tides, there is a peculiar and characteristic zone called appropriately by Stephenson *et al.* (1937) the "sublittoral fringe." The characteristic algae are probably restricted at their upper limits by desiccation, and at their lower limits by deficient illumination. Wave action is maximal here, and the larger brown seaweeds (*Himanthalia, Alaria, Laminaria digitata*), as is frequently pointed out, are well adapted by their pliable stipes to withstand sudden and violent stress. Perhaps of equal importance is the fact that at low tides they lie prostrate and so in the main escape desiccation. After low spring tides in very hot dry weather I have seen the fronds of *Laminaria digitata* around Carsaig Island scarred with dead patches where they had projected from the water. However, at greater depths these algae of the sublittoral fringe cannot compete with the erect and less pliable *Laminaria Cloustoni*. It is noteworthy that *L. digitata* fails to penetrate the true sublittoral region except as an epiphyte of *L. Cloustoni;* by this means it borrows the advantages of a tall erect stipe and achieves "a place in the sun." On the other hand, *L. Cloustoni*, though a true sublittoral form, may by its habit of growth expose its frond to the dangers of emersion at low water of spring tides, and is, in fact, quite probably limited by desiccation. The animals of the sublittoral fringe are restricted at their upper limits by exposure to air, but in general range downwards extensively into the shallow sublittoral, since they are less dependent on light than are the algae. However, in certain cases immersion may possibly be detrimental (Moore and Kitching, 1939).

In the sublittoral region proper the upper limits of distribution of organisms are determined by excessive wave action, and perhaps by excessive illumination in some cases; whereas the lower limits are set by deficient wave action and deficient illumination. The factors effective in controlling zonation below the sublittoral fringe are not steeply graded, and therefore zonation is not sharply marked.

The limitation of the vertical distribution of sublittoral organisms by wave action can be demonstrated readily, because in such cases these limits are raised where the coast-line provides greater shelter, depressed where it is more open to the waves. The upper limits of *Laminaria saccharina,* in its sea-loch form, and the lower limits of *Membranipora membranacea* and *Obelia geniculata* (see p. 327) are examples. The effect of wave action upon marine organisms is complex and obscure; and the amount of wave action necessary to support the existence of an organism may depend on other environmental conditions (Moore and Kitching, 1939). Apart from its destructive mechanical effect, wave action probably influences the settling of larval forms, promotes the circulation of planktonic food, disturbs sediment, and obliterates extreme fluctuations in the physical and chemical conditions of the water.

Limits of distribution determined by illumination, in contrast to those set by wave action, are likely to be relatively independent of the conformation of the coast-line over a small area, despite local variations in the loss of light at the surface of the water. The transition from the sublittoral fringe to the zone of *Laminaria Cloustoni* involves a decline in illumination at the sea botttom so great and so steep that none of the chief undergrowth-forming algae is common to both levels. However, within the broad *L. Cloustoni* zone, the illumination is by comparison almost uniformly dim, and over a range of 12 meters no case was found in which limitation could be attributed to illumination. Although the upper limits of the shade-loving undergrowth algae of the *L. Cloustoni* zone coincide with a sudden gradient of illumination, yet it is not clear whether these algae are restricted directly by excessive illumination, or by some other factor, such as a brief exposure during low equinoctial spring tides. It has been shown that in certain of these algae, *Delesseria sanguinea* and *Plocamium coccineum* (Moore, Whitley and Webster, 1923), and under certain conditions, the greatest photosynthetic activity takes place under moderate rather than very strong illumination; but for present purposes much more experimental evidence is required. It must also be remembered that this discussion is concerned throughout with organisms in competition, and that competition is likely to accentuate the sensitivity of these organisms to their environment (Beauchamp and Ullyott, 1932).

It is important to recognize that not only the quantity but also the quality of the light varies with depth. Green and blue light,—in coastal waters especially the former,—penetrate more readily than orange, red, and ultra-violet; and therefore with increasing depth they predominate to an ever-increasing extent (see the review by Clarke, 1939). Atkins (1926) has stressed the importance of this change in quality in relation to the vertical distribution of algae. In spite of certain obvious exceptions, it is in general true that green and brown algae are restricted to littoral and shallow sublittoral levels, whereas many red algae penetrate to greater depths. For instance, red algae have been dredged in the English Channel (Hamel, 1923) and off the Faeroes (Børgesen, 1908) from depths of 45 and 50 meters respectively, whereas the brown algae do not in general extend below 25 meters in Faeroese waters. At the depths to which red algae penetrate the light is mainly blue and green. It has been suggested (for references see Atkins, 1926) that by the nature of their photosynthetic pigments they derive the greater part of their energy from light of these colors; and this hypothesis may be applied with reasonable safety to algae growing at depths where green and blue light vastly predominate. However, various of these shade-loving red algae, *Phycodrys rubens, Delesseria sanguinea, Ptilota plumosa,* found at 40–50 meters off the Faeroes, are characteristic of the undergrowth of the *Laminaria* forest in the shallow sublittoral region, and are also found in sea caves (Børgesen, 1908; Rees, 1935). This implies a wide tolerance of variations in the spectral composition of the light. In spite of qualitative differences in illumination, there is clearly an ecological similarity between the shades of the *Laminaria* forest, the half darkness of caves, and the open sea bottom of the deeper sublittoral region. The incidence of green and blue light is probably of the same order in the deeper sublittoral and in the *Laminaria* forest (Table III).

TABLE III

Color of light	Blue	Green	Light red	Dark red
Range of filters (approximate)	350–470 mμ	500–570 mμ	620–700 mμ	700–750 mμ
Transmission per meter (see Fig. 4)	83%	90%	59%	27.5%
Depth at which monochromatic light intensity is equivalent to 1% of that in *Laminaria* forest near low water mark	25 meters	40 meters	10 meters	3 meters

Although this suggests that within the *Laminaria* forest the green and blue light alone are sufficient to support the shade-loving red algae, it still remains uncertain to what extent use can be made of light of other colors. It seems possible from the work of Klugh (1931) that some at least of the deeper water red algae, though able to make an exceptional use of green light, may nevertheless be able to utilize profitably a considerable range of the spectrum. Much more work is needed on this subject.

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SUMMARY

1. On the shores of Carsaig Island, Scotland, the sublittoral region is densely forested with laminarian seaweeds down to a depth of at least 15 meters, and probably down to a much greater depth.

2. At the upper margin of the sublittoral region, exposed to air at low water of spring tides, there is a characteristic " sublittoral fringe."

3. The dominant brown algae of the sublittoral fringe have pliable stipes, so that they lie flat at low water and escape desiccation. The dominant brown algae of the true sublittoral region have tall erect stipes, which hold up the fronds to the light.

4. The *Laminaria* canopy at depths of 1–6 meters cuts off about 99 per cent of the available light. At 6–12 meters the forest is less dense, and relatively more light penetrates. There is therefore a sharp decline in illumination between the sublittoral fringe and the *Laminaria* forest just below it; but within the forest the illumination changes much less over a considerable range of depth.

5. Wave action is considered to be maximal in the sublittoral fringe, and to decrease gradually with depth.

6. The undergrowth-forming algae fall into two clearly defined groups—one group confined to situations of high illumination, such as the sublittoral fringe and the upper parts of *Laminaria* stipes; and the other to dark places, such as the rock surface in the depths of the forest and the lower parts of the *Laminaria* stipes.

7. The undergrowth of the *Laminaria* forest is practically uniform in composition within a vertical range of about 12 meters, and probably more.

8. Vertical distribution is determined chiefly by wave action in the case of one laminarian alga, two polyzoa, one hydroid, and probably other organisms.

9. It was found that on artificially denuded areas new *Laminaria Cloustoni* plants grew to form a forest 1 meter high in 12 months.

10. It is concluded that whereas the steeply graded zonation of the littoral region is to be ascribed in the main to desiccation, the more gentle zonation of the sublittoral region depends on illumination and on wave action.

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